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THE EVOLUTION OF FLOWERS

By JOHN H. LOVELL

WALDOBORO, MAINE

WHAT is a flower? This would seem to be an easy question for a botanist to answer; but, as a matter of fact, the definitions differ widely, and it has even been asserted that a strict definition is impossible. According to the German morphologist, Goebel, a flower is simply "an axis bearing sporophylls," that is, a stem with one or more modified leaves bearing spores. The fructifications of the horsetails and club-mosses would thus be regarded as flowers. This extension of the term is certainly not without its advantages, since it calls attention to the very ancient origin of floral structure and to its beginning among the primitive forms of plant life; but the strobili of the Pteridophytes are so unlike those of the Angiosperms and are so much older that to call both flowers is likely to prove confusing. Asa Gray and the older morphologists often speak of "the flowers" of the Gymnosperms; but the open carpel without style or stigma, as well as a difference of opinion in the case of several groups as to what constitutes a flower and what an inflorescence, are objections to this usage. Consequently it has been proposed to restrict the word flower to the Angiosperms, plants with a closed carpel, a part of which is specialized for receiving pollen. The term, as thus limited, has a very definite meaning, which can not be easily misunderstood even when the flower is reduced to a single stamen or pistil as among the aroids. This definition has also the advantage that it agrees with the popular conception of the word; and where possible for obvious reasons it is desirable that the definitions of science and of the non-scientific public should agree. The Angiosperms have been well called the Anthophyta, or flower-plants.

In the history of the evolution of plants the origin of the Angiosperms still remains an unsolved mystery. This great series makes its appearance suddenly in the Lower Cretaceous; and the fossil species exhibit no intermediate or transition stages, but possess all the essential characters of their modern representatives. There are a variety of comprehensive forms, it is true, which have been termed Proangiosperms; but there is no certainty that any of them are the actual precursors from which sprang the plants with a closed carpel. If, however, the Proangiosperms *de factu* were trees, as has been strongly advocated, there is good reason to hope that this knowledge will not always remain a secret of the rocks. But for the present any attempt to trace the

phylogeny of the Angiosperms must rest largely upon comparative morphology and conjecture; and so great is the fascination the problem offers that it is no exaggeration to say that every probable and improbable guess has been exhausted.

Vines formerly advanced the opinion that the Dicotyledons were descended from the conifers and the Monocotyledons from the cycads. Miss Benson, Hallier and Karsten have endeavored to trace back the Angiosperms, through the ament-bearing trees (Amentaceæ), to *Gnetum* of the Gnetales, an aberrant group of Gymnosperms. Campbell has suggested that the Monocotyledons may be connected with forms like *Isoetes*, as both have a single first leaf, and there are resemblances in the anatomical structure of the stem, leaf and root; but, he adds, that there is an immense interval between the simplest angiospermous flower and the sporophylls of *Isoetes*. Coulter has pointed out that *Selaginella* in its dicotyledonous embryo and the resemblance of the megasporangium to the seed condition is as suggestive of the Dicotyledons as *Isoetes* of the Monocotyledons; but an independent origin of both groups from *Marattia*-like ferns is favored. Others would reject a derivation both from the Gymnosperms and fernworts and seek for the beginning of the Angiosperms among the Bryophytes, or as a wholly independent phylum arising from the Algæ—one highly imaginative theorist, for instance, would derive the higher seed plants from the liverworts through apospory.

If these widely ranging speculations, of which only a very few are cited here, prove anything, it is that at the present time it is futile to look for the origin of the Angiosperms outside of the Gymnosperms. If they have come from a more primitive source, then we must be content to wait until the geological record shall be further revealed. As for the Gymnosperms themselves, it is established with reasonable certainty that they are descended from the Pteridophytes; and that their evolution extended over a long period of time, during which a great number of species became extinct. During the Mesozoic Age more especially in the Triassic, a remarkably equable climate prevailed over a large extent of the land surface of the globe, and gymnospermous trees were the dominant forms of plant life; conifers, maidenhair trees, cycads and cycadophytes in the greatest variety multiplied and developed every possible combination of cone structure. These vast forests must have displayed a foliage which in beauty of form has never been equalled, either before or since, in a terrestrial landscape. To suppose that contemporaneously another great phylum, which gave birth to the Angiosperms, was in existence, but of which not a vestige has been discovered, seems at least improbable. The morphological differences between the Angiosperms and the Gymnosperms, it is true, are so great that there is a strong tendency to regard them as entirely independent, nevertheless

the affinities between these two great series are much closer than between the Angiosperms and the Pteridophytes, *e. g.*, there can be no doubt, as Jeffrey insists:

> That the argument for descent from the Gymnosperms seems to gain great force from the entire absence of fernwort characters in the shorter leaves of the Angiosperms.

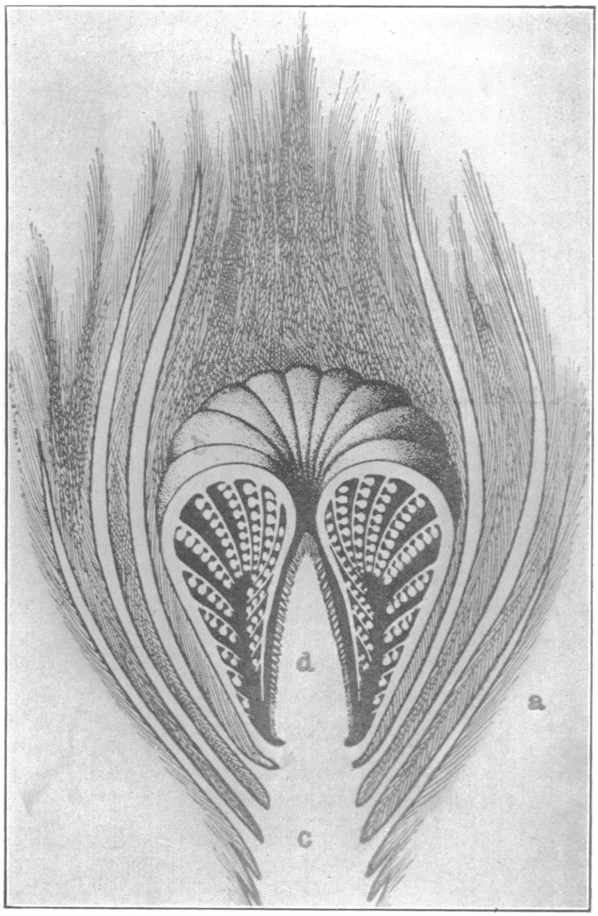

DIAGRAM OF STROBILUS OF *Cycadeoidea dacotensis.* (After Wieland.) *a*, hairy sheathing bracts; *b*, folded stamens; *e*, elongated axis; *d*, conical mass of sterile and fertile scales.

A few years ago the gymnospermous origin of the Angiosperms was temporarily believed by many to have been fully established when Wieland published his description of the bisporangiate cone of *Cycadeoidea dacotensis,* a fossil plant belonging to the extinct order Bennettitales. It was not supposed that *Cycadeoidea* was the direct ancestor of

the Angiosperms, but that the structure of its strobilus furnished decisive evidence of their derivation from an allied group as yet undiscovered. It was confidently hoped that the baffling mystery of the descent of the Anthophytes was about to be solved; and Arber and Parkin, taking Wieland's investigations as the basis of their work, sought to reconstruct the ancestral type of such flowers as *Magnolia.* The characters of the strobilus of *Cycadeoidea,* in the opinion of Scott, justify the conclusion that the Bennettitales were, of all known plants, the most nearly akin to the Angiosperms. The fructification of *Cycadeoidea,* which created a genuine sensation in the botanical world, must thus be regarded as the most interesting "flower" known to-day.

The strobilus of *Cycadeoidea,* as described by Wieland (see Fig. 1), was nearly five inches in length, with an elongated axis on which all the floral members, except the stamens, were spirally inserted. A series of densely hairy sheathing bracts, about three inches long, represented a primitive perianth. The bipinnate, frond-like stamens were united at base into a disc, and on the numerous pinnae there were two rows of pollen-sacs. The apex of the conical axis, prolonged above the stamens, was covered with a mass of fertile and sterile scales. The fertile scales were reduced to long slender stalks bearing terminal seeds containing dicotyledonous embryos. The interseminal sterile scales were club-shaped at the end and united by their distal edges into an envelope resembling a pericarp with a small central orifice out of which projected the micropyle, or open end of the seed. The flowers were anemophilous and the pollen came directly in contact with the seeds as in other Gymnosperms. If the large cones of this species, or of other Cycadophytes, displayed dull red or purple coloration, as is the case with many modern conifers and cycads, the Mesozoic forests were not entirely a somber monotonous green as is commonly supposed.

Guided by the strobilus of *Cycadeoidea* Arber and Parkin have endeavored to reconstruct the prototype of an angiospermous flower like *Magnolia.* This hypothetical "flower," or strobilus, is supposed to have been of large size, solitary, with the members spirally arranged on an elongated axis. The perianth was composed of an indefinite number of leaf-like bracts, which were probably green in color. The staminate organs may have been bi-pinnate fronds bearing two rows of pollen sacs upon the lateral leaflets; but it is more probable that they were very much reduced in size and that the lateral pinnæ had disappeared,—fossil stamens of a *Williamsonia* found by Wieland in Mexico had the number of pollen sacs reduced to two. The central fertile scales were broad, short leaves bearing a few ovules on their margins, a primitive stage still preserved by the carpellary leaf of *Cycas.* The strobili were pollinated by the wind as in all other Gymnosperms of this age. The effective

factor in transforming this ancestral form into a flower like *Magnolia*, according to Arber and Parkin, was the establishment of entomophily or insect visits. From this assumed prototype a *Magnolia* flower differs chiefly in that the stamens have lost their leaf-like character and bear only two anthers, while the open carpels have folded over the seeds and the pollen is received on a stigmatic surface. To both types are common the large size, the elongated axis and the spiral arrangement of the organs, except in the perianth of *Magnolia*, where the cyclic order might easily have been derived from the spiral.

In whatever light this hypothesis may be regarded, it is, at least, certain that the fossil *Cycadeoïdea* never gave rise to an angiospermous species. The foliage alone presents almost insuperable difficulty, for while the Cycadophytes had simple bulbous or columnar trunks, surmounted by a crown of fern-like leaves, the Angiosperms branch freely and are microphyllous. Insects could not have been instrumental in bringing about such a transition; and Arber and Parkin endeavor to bridge the difficulty by the improbable supposition of a saltation or mutation. It is much more probable that the varied foliage of the Angiosperms finds an explanation in its physiological significance. Neither does the internal anatomy nor the structure of the gametophytes, according to Jeffrey, lend support to such a relationship. The carpel of *Cycadeoidea* is as truly gymnospermous as that of the cycads or conifers and is even more reduced, remaining only as a slender stalk; while the so-called pericarp, formed by the sterile scales, is not at all homologous with the closed carpel of the Angiosperms. But undoubtedly the strobili of the Bennettitales are helpful in suggesting the structure of the veritable Proangiosperms, which appear to be at present wholly unknown.

As already stated, Arber and Parkin regard the establishment of entomophily as "the motive force," which called the Angiosperms into existence and laid the foundation of their future prosperity. Scott likewise holds "that the rise and progress of the Angiosperms was probably due, above everything else, to their adaptation to the contemporary insect life." This is the generally accepted view, from which there seems to have been expressed no difference of opinion; but it is noteworthy that this theory was advanced chiefly by paleobotanists without extensive field experience in the observation of the phenomena of flower pollination. The reciprocal relations of flowers and insects are often truly wonderful and floroecology doubtless embraces more of romance than any other branch of botany. Entomophily could hardly fail to make a deep impression on the imagination of phylogenists in search of "motive forces"; but in the writer's opinion as a factor in the development of angiospermy it has been greatly overworked and forced to bear a burden greater than it can carry. As a matter of fact there probably were no insects deserving to be called anthophilous contemporaneous

with the beginning of the higher seed plants. Angiospermy must have arisen previous to the Cretaceous; and in the Cretaceous rocks the remains of very few insects have been found, the highest forms in America being those of beetles. As pollinators of flowers the Coleoptera are of little significance; and the development of the entomophilous flora would not have varied in any way in the absence of all anthophilous beetles. There seems to be no reason to suppose that flowers were visited by insects in the Jurassic Age, or that suitable species were in existence. The habit of anthophily was not quickly established; and it was long after the appearance of the primitive Angiosperms that the bees and butterflies were evolved.

But assuming, for the sake of argument, that there were anthophilous insects contemporaneous with the wind-pollinated Proangiosperms, let us inquire whether they could have induced the closing of the carpel. *Welwitschia,* a genus of the Gnetales, is entomophilous, but it still remains a Gymnosperm. If there are African cycads pollinated by insects, as Scott thinks probable, it has not led to angiospermy; nor is there any tendency toward such a modification in several living conifers which are frequently visited by beetles for pollen. Neither would the sporadic visits of unspecialized insects to the progenitors of the Angiosperms have been likely to have resulted in the development of angiospermy. The primitive open carpel must have been either uniovulate or multiovulate. If it were multiovulate then so long as it remained unclosed wind-pollination would have been more effective than insect-pollination, since the wind would be more likely to bring the requisite amount of pollen to many naked ovules than to a small stigmatic surface. The wind would also be a more reliable agent than the erratic visits of primeval insects, which might very rarely come in contact with the ovules of large strobili or of monosporangiate cones. In the case of the multiovulate carpel, so far as pollination in this age was concerned, the advantage would be greatly on the side of the open carpel and anemophily.

If, however, the carpel were uniovulate then obviously it could be equally well pollinated by the wind or insects, whether closed or open, indeed a lobed papillose stigma would offer a larger surface to the wind than would the micropyle of a single ovule. The inclosing of the carpel would here be independent of the question of pollination. For this reason the writer believes that the proangiospermous carpel was uniovulate, as it still is in many anemophilous and entomophilous primitive Angiosperms, *e. g.,* the wind-pollinated grasses and sedges, and largely in the Amentaceæ, and in the entomophilous *Alisma, Ranunculus* and *Fragaria.* In this connection it is noteworthy that the achenes of the Compositæ are one-seeded. The wide occurrence of uniovulate carpels among living Angiosperms would indicate that it was the prevalent

condition among the Proangiosperms, a conclusion supported by the commonness of carpels with a single ovule among the Gymnosperms. If the reverse had been true, it is highly improbable that the number of ovules would have been reduced after the establishment of entomophily; in the Ranunculaceæ the carpels of the primitive genus *Ranunculus* are uniovulate, while in the more highly specialized and later evolved genera *Aquilegia, Delphinium* and *Aconitum,* which are pollinated by bumblebees, the carpels are many seeded. One of the conditions, we hold, then on which the rise of Angiospermy was dependent was the uniovulate open carpel, which was equally well pollinated by the wind or by insects.

The rise of angiospermy was, therefore, independent of insects antedating the appearance of the anthophilous species, the visits of which did not become important until the higher seed plants were fully differentiated and the fundamental characters of foliage and flower determined. If the great plant groups the Cycadofilacales, Cordaitales, Cycadales, Bennettitales and Coniferales were successively evolved under anemophily, there is no inherent improbability in the Angiosperms also originating under wind-pollination.

Since the infolding of an uniovulate open carpel would be of no special benefit in pollination, and angiospermy has not been induced by entomophily it is very pertinent to inquire, in response to what conditions is it a reaction? It is undoubtedly one of the many structures, which have been developed to afford protection to the ovules and seeds in their various stages of growth. Cowles says:

> Adequate protection is especially important in monocarpic species, above all in annuals, since the maintenance of the species depends absolutely upon the viability of its seeds.

Throughout the spermatophytes the need of protection to the seeds is constantly emphasized. In the Cycadofilacales, where the ovules were borne directly on the margin of the sporophyll, they were often enclosed in husks or cupules. In the Cycadales, with the exception of *Cycas,* they are covered by the closely appressed cone-scales; while in *Cycadeoidea* protection was afforded by sterile, club-shaped, interseminal scales. In the Coniferales the seeds are on aborted shoots in the axils of the cone-scales, an advantage of so much importance that Saporta and Marion attribute the existence of the conifers to the development of the cone. Although Arber and Parkin regard angiospermy as a response to entomophily, they at the same time recognize that the closed carpel offers effective protection to the developing ovules. In the Proangiosperms small, uniovulate, open carpels were crowded on the apex of an elongated axis, as in *Magnolia,* where protection to the nascent ovules was most readily secured by the infolding of the carpel.

The involution of the carpel offers in itself very little difficulty, and there are numerous petals and leaves, which regularly or occasionally illustrate the origin of this modification. Abnormal cohesion of the margins of leaves is not unusual, and has been observed in the genera *Tilia, Corylus, Pelargonium* and *Antirrhinum,* and in the leaflets of the rose and strawberry. Phyllody of the pistils or their reversion to open leaves bearing ovules on their margins has likewise been recorded of many species. The protection of nectar from rain or useless insects has given rise to a great variety of tubular petals. In *Ranunculus auricomus* every intermediate stage between the open petal and the tubular nectary occurs; and in *Eranthis hyemalis* there is present a series of transitions between the outer flat perianth segments and tubular petals. Tubular petals are in some flowers the normal condition as in *Helleborus;* and they may occur where this form is apparently useless. Changes from strap-shaped to tubular corollas may often be observed in the marigold and aster; while in *Coreopsis tinctoria* one variety regularly has the rays tubular. In a variety of *Papaver bracteatum* the petals cohere to form a gamopetalous corolla. Undoubtedly tubular nectaries have been developed independently in widely separated families; and it is not improbable that angiospermy may have originated more than once. The carpel did not at first close entirely, but the apex was filled with a mucilaginous liquid, which served to retain the pollen until the development of a stigmatic surface—such a mucilaginous drop is found in the micropyle of coniferous ovules. The subsequent development of the style permitted the relative position of the stigma to be changed; the filaments performing a similar service for the anthers.

How long an interval elapsed after the origin of angiospermy before entomophily was established it is impossible to say; but the evolution of the bees, or Anthophila, the most important of all the anthophilous groups, must have been a comparatively modern event. The first flower-visiting insects were synthetic types without special adaptations for gathering pollen or nectar; and their attentions were, of course, forced upon flowers and not the result of allurements offered to secure their services. In the writer's opinion pollen was the first source of attraction. To suppose that the fructifications of the Proangiosperms contained nectar is purely an assumption, since there is no reason to believe that the strobili of the anemophilous Gymnosperms were ever nectariferous, or that nectar was common in flowers until after the rise of entomophily. Moreover, an examination of anthophilous insects shows that they became progressively specialized from pollen-eaters to nectar-feeders. Of the beetles seeking flower food *Trichius affinis, Euphoria inda* and various Coccinellidæ manifest a preference for pollen; while the genera *Nemognatha* and *Gnathium* live wholly on nectar, for procuring which the maxillæ have become modified into a suctorial tube.

Among Diptera the Syrphidæ and Muscidæ consume both pollen and nectar, while the Bombylidæ and Empididæ feed entirely on nectar. The short-tongued bees belonging to the genera *Prosopis, Sphecodes, Halictus* and *Andrena* still eat pollen; but adult honey-bees are wholly dependent on honey, and in its absence a colony will starve although there is an abundance of pollen in the combs. The evidence favors the view that anthophilous insects began by eating pollen, and that the secretion of nectar and its use as a food were events of later date. In their relations to a floral diet, adult beetles and flies may be divided into four groups: (1) species which never visit flowers or only accidentally; (2) species which are partly predaceous or phytophagous and partly anthophilous; (3) species which live on pollen and nectar exclusively; (4) species which live on nectar alone.

The pollen of anemophilous flowers is still gathered by both the smaller and larger bees and devoured by beetles and flies. According to Henslow there is no pollen grain so smooth that the hairs on the limbs of a bee or fly can not hold it, even the pollen grains of grasses, though smooth in water, when dry are notably wrinkled into sharply angled and irregular shapes. Small Syrphid flies have been observed by the writer resorting regularly in the morning to the flowers of the common herd's grass for the purpose of feeding on the pollen. While honey-bees to-day more often gather pollen from anemophilous flowers than the solitary wild bees, this is obviously an artificial relation incidental to the many large apiaries maintained for the production of honey and wax, which contain thousands of workers and require immense quantities of pollen for brood-rearing. At the time of the beginning of entomophily the Anthophila were not in existence. Unlike all other tribes of insects, the bees are wholly dependent on pollen for brood-rearing, and the acquisition of this habit must have been an important factor in determining the course of their development. The pollen of entomophilous flowers has acquired adhesiveness and a rough or spinose surface, which greatly facilitates its transfer by insects from one flower to another.

While insects were first attracted to flowers by pollen, nectar secretion offered a stronger allurement and gave a new impulse to entomophily. Nectaries occur on the foliage of a great variety of plants, even on the stalks of ferns (*Pteris*), as well as in flowers; and its secretion is primarily a function independent of insects. Leaves secrete and excrete a great variety of products, and besides nectar glands may possess water-glands, chalk-glands and slime-glands. Since transitions between water-glands and nectar-glands occur, it can not be certainly affirmed, says Cowles, that the secretion of nectar by leaves is other than a waste product. The appearance of nectar-glands, at least occasionally, on the modified leaves of entomophilus flowers would be wholly in accordance with expectation; and their value in attracting insects would ensure

their preservation. The need of protection from wet and robber insects subsequently resulted in the development of nectaries. In more recent times this function in my opinion has been lost by various pollen flowers, as *Anemone, Rosa* and *Desmodium,* and nearly so by the mulleins.

Besides an adhesive pollen and nectar secretion there are correlated with entomophily bright coloration, attractive odors, and a great variety of mechanisms for the transfer of pollen through insect agency. Except to a very limited extent these characters do not belong to wind-pollinated flowers, and in the absence of insects there is no satisfactory evidence that they would have ever been developed. On the contrary with the cessation of insect-visits they may be speedily lost and the flowers revert to anemophily, as in *Artemisia.* Among the older floroecologists it was practically the universal belief that the structural modifications enumerated were purposive adaptations to ensure cross-pollination. Adaptation in this sense is now regarded as akin to vitalism and its validity denied. It may be admitted that plants do not possess an inherent power of producing structures because they are needed, that natural selection has been given too wide an application, that other factors have been important in the development of flowers, as orthogenesis, mutation and, in view of the probability that many species are hybrids, as held by Lotsy and Jeffrey, Mendelian laws of inheritance. But while many minor and extreme structures of flowers may be due to special factors, the hypothesis that the general trend of floral evolution has been determined by the preservation of advantageous variations, whatever their origin, by natural selection offers the field ecologist a tenable working theory better than any other available.

Difficult as is the problem of the origin of flowers, a solution is far from hopeless.

> By past efforts unavailing,
> Doubt and error, loss and failing,
> Of our weakness made aware,

there is nevertheless no other course left for the phylogenist than to continue "trying with uncertain key door by door of mystery." The great success of the paleobotanist in tracing the descent of the Gymnosperms awakens the hope that fossil records will yet be discovered, which will throw new light on the evolution of the Anthophytes. Let us await the testimony of the rocks.